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Earthworms modulate the effects of climate warming on the taxon richness of soil meso- and macrofauna in an agricultural system

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ABSTRACT

Anthropogenic climate change is altering the functioning of terrestrial ecosystems. Agricultural systems are particularly vulnerable to climate change as they are frequently disturbed by intensified management practices. This also threatens belowground organisms that are responsible for providing crucial ecosystem functions and services, such as nutrient cycling and plant disease suppression. Amongst these organisms, earthworms are of particular importance as they can modulate the effects of climate change on soil organisms by modifying the biotic and abiotic soil conditions. However, they are also known to decline under intensified management, justifying their use as key biotic indicators of intensified agriculture. Yet, our knowledge of the responses of belowground species to the interacting effects of warming and land-use intensification (simulated by earthworm reduction in the experimental setup) remains limited. Here, we tested the interactive effects of soil warming and reduced earthworm densities on soil protists, nematodes, meso- and macrofauna, and their diversity in a common barley system in the Hohenheim Climate Change Experiment. We found that belowground species richness was lowest at elevated temperature and reduced earthworm densities, indicating that earthworms can buffer warming effects on belowground biodiversity. Furthermore, warming increased the densities of plant-feeding nematodes, and herbivorous macrofauna benefitted from reduced earthworm densities. Our results indicate that warming and reduced earthworm densities may simultaneously modify the functioning and service provisioning of soils via shifts in diversity and density of soil biota that would likely lead to simplified belowground food webs. These findings thus highlight the importance of maintaining greater densities of ecosystem engineers like earthworms that may help buffering the detrimental effects of climate warming in agricultural systems.

1. Introduction

Ecosystems worldwide are under unprecedented stress due to anthropogenic alterations of climatic conditions (Masson-Delmotte et al., 2018) and changing land-use practices (Newbold et al., 2015). As a result, species composition and ecosystem functions are dramatically changing in natural and managed ecosystems (Walther et al., 2002; Kardol et al., 2010b). In Central Europe, arable lands are amongst the most important managed terrestrial ecosystems (Howden et al., 2007). They are crucial for maintaining global food security (Pachauri et al., 2014). These systems are also highly disturbed owing to management practices like tillage and heavy machine employment, which potentially convert them to low diversity ecosystems (Giller et al., 1997; Tsiafouli et al., 2015). Owing to their low numbers of component species,

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agricultural systems are additionally vulnerable to ongoing anthropogenic climate change as low diversity systems have reduced resistance and resilience to external environmental stresses (Yachi and Loreau, 1999; Isbell et al., 2017). While most studies have focused on the responses of aboveground species diversity and associated functions in response to global changes in agricultural systems (Lobell et al., 2008), comparable knowledge on belowground biodiversity is still lacking.

Several studies have consistently shown that belowground species diversity is crucial for ecosystem functioning and the provisioning of ecosystem services (Orrell and Bennett, 2013; Bardgett and van der Putten, 2014; Wagg et al., 2014). Agricultural ecosystems are no exception. For instance, Wall et al. (2015) highlighted that soils with greater diversity of soil biota are key to maintain higher levels of food production in agricultural systems. Greater diversity of soil biota helps to suppress pests and diseases of plants, enhances nutrient cycling, and thereby improves both crop production and quality (Lavelle et al., 2006; Brussaard et al., 2007).

Soils are characterized by a vast pore system with extensive surfaces, enabling a great variety of organisms to colonize water films and hotspots of resource availability (Coleman et al., 2004), as long as soil structure is left intact (Bronick and Lal, 2005). However, higher soil temperatures in response to climate warming are known to reduce soil water content (Poll et al., 2013). This threatens many soil organisms that rely on these moist environments for their survival, as their integuments are often permeable to water (Coleman et al., 2004). Based on this strong water dependency, the abundance and diversity of many taxa are known to decrease with drought and warming under global climate change (Blankinship et al., 2011; Geisen et al., 2014), due to detrimental effects on their physiology, development, and reproduction (Lindberg, 2003). This is one of the reasons why soil organisms are particularly susceptible to climate warming but also to agricultural management techniques that constantly destroy the soil structure by homogenization and shifting of soil layers and potential habitats. For example, it was shown that agricultural intensification negatively affects many groups of soil organisms (Gardi et al., 2008), like ground beetles (Purtauf et al., 2005), spiders (Birkhofer et al., 2008), mites or springtails (Tsiafouli et al., 2015). Thus, on-going agricultural intensification and climate warming pose unprecedented threats to belowground biodiversity likely via complex interactions among rising temperature, soil drying as well as losses in soil structure (Allan et al., 2014; Tsiafouli et al., 2015).

One of the key biotic indicators of intensive agricultural management is the density of earthworms (Edwards and Bohlen, 1996; Pelosi et al., 2014). Agricultural intensification can substantially reduce earthworm density by tillage and excessive use of pesticides and mineral fertilizers (Paoletti, 1999; Decaëns and Jiménez, 2002; Smith et al., 2008). Earthworms are further expected to decline under drought stress in a warmer world (Eggleton et al., 2009). Earthworms contribute to several important functions in terrestrial ecosystems. For instance, by bioturbation (i.e., burrowing, casting, ingestion of soil, mixing litter and soil) these ecosystem engineers shape the biotic and abiotic conditions in the soil, which are crucial for the abundance and diversity of other soil biota (Edwards and Bohlen, 1996; Eisenhauer, 2010) and crop productivity (van Groenigen et al., 2014). In particular, earthworms affect the structure of soil food webs by usually promoting other smaller soil decomposer species, such as collembolans, by increasing habitat heterogeneity and resource availability (Eisenhauer, 2010). Thus, a decline of earthworm densities can have far-reaching consequences for plant productivity (van Groenigen et al., 2014), soil food web structure (Eisenhauer, 2010), pest control (Pelosi et al., 2014), and food security (Bertrand et al., 2015).

The presence of earthworms can further determine the ability of soil communities to cope with the effects of climate warming (Eisenhauer et al., 2012; Lubbers et al., 2013). For instance, earthworm activity can ameliorate the detrimental warming effects by creating refuge areas in the soil, where particularly smaller soil organisms can find shelter and food resources to escape desiccation and survive drought periods (Eisenhauer, 2010). This implies that as long as high earthworm densities are maintained, detrimental effects of warming and intensified management on soil biota could be minimized to a certain extent. However, earthworms have also been shown to intensify climate change effects on soil biota, e.g., by drying out the top soil in warmer environments as they create preferential water flow pathways (Shipitalo et al., 2004; Eisenhauer et al., 2012).

Based on these future scenarios of climate warming and land-use intensification in agricultural ecosystems, we tested the interactive effects of experimental soil warming and reduced earthworm densities (as one important aspect of intensified agricultural management) on the abundance and diversity of soil organisms in a common barley agricultural system in the Hohenheim Climate Change Experiment (HoCC) in South West Germany. We measured aboveground plant biomass, soil microbial biomass, and the abundances of a large group of soil biota ranging from protists and nematodes to soil meso- and macrofauna to explore their responses to increasing temperatures and reduced earthworm densities. We hypothesized that (i) warming reduces the abundance and diversity of soil organisms due to their high vulnerability to warming-induced water stress, (ii) earthworms increase the abundance and diversity of soil organisms, e.g. by postulated mechanisms like enhancement of the spatial heterogeneity of resources and refuge areas for soil organisms in the disturbed agricultural soil, and thus (iii) earthworms buffer the negative effects of warming on soil organisms.

2. Methods

2.1. Site description

The Hohenheim Climate Change Experiment was established in 2008 on an arable field at the experimental Station Heidfeldhof (N48°42′50″ E009°11′26″, 395 m a.s.l.) of the University of Hohenheim. The soil is a loess-derived stagnic Luvisol with silty loam-texture (Ap horizon: pH 7.0; organic carbon content: 12.1 g kg^{-1}; bulk density: 1.28 g cm^{-3}). The Hohenheim meteorological station nearby recorded a mean annual temperature of 8.9 °C and a mean annual precipitation of 622.2 mm for 2010 (the year of the study).

2.2. Experimental design and treatments

The Hohenheim Climate Change Experiment had a randomized block design with four blocks, in which the earthworm and temperature treatments were crossed (Poll et al., 2013). To study the interactive effects of experimental warming and earthworm density, 16 subplots were established (1 m^2 each). There were four treatments with four replicates each: 1) ambient temperature and ambient earthworm density, 2) ambient temperature and reduced earthworm density, 3) elevated temperature and ambient earthworm density, and 4) elevated temperature and reduced earthworm density (Fig. S1). The treatments were realized by experimental soil warming (ambient + 2.5 °C; measured at a soil depth of 4 cm) and a reduction of earthworm densities. The temperature treatments were chosen according to predictions of temperature change in the study region for the end of the 21st century (Umweltbundesamt, 2006; IPCC Synthesis Report, 2007). For increasing the soil temperature, heating cables (RS 611–7918, RS Components GmbH) were installed on the plots with elevated temperature in July 2008, and dummy cables were installed in non-heated plots as experimental controls. The cables were placed on the soil surface in 3–4 cm distances covering the full plot area. They were permanently in use with only short interruptions during tillage (when they were removed from the plots and reinstalled afterwards). Data loggers (DT85, UMS GmbH), which were connected to temperature probes in 4 cm soil depth, logged and controlled the temperature every minute and regulated the electricity supply of the heating system according to the target

temperature increase of 2.5 °C compared to the ambient treatments.

At the beginning of the HoCC experiment (in May 2008, the reported study took then place in 2010), earthworm densities were assessed on the arable field. On average, 124 individuals were found per m^2. About 94% of the earthworms were juveniles. In total, five earthworm species were found: *Lumbricus terrestris* (Linnaeus, 1758), *Aporrectodea longa* (Ude, 1885), *Aporrectodea caliginosa* (Savigny, 1826), *Aporrectodea icterica* (Savigny, 1826) and *Aporrectodea rosea* (Savigny, 1826). During the establishment of the HoCC experiment in May 2008 and when the soil was ploughed (November 4th 2009), all visible earthworms were removed from plots assigned to the earthworm reduction treatment by hand sorting down to a soil depth of 30 cm. In addition, earthworm densities were reduced in spring 2009 (April 1st and 2nd) and 2010 (March 24th) by using the octet method (Thielemann, 1986; Eisenhauer et al., 2009), by which earthworms are extracted without disturbing or contaminating the soil (Weyers et al., 2008). Four octet devices (DEKA 4000, Deka Gerätebau, Marsberg, Germany) were used for 35 min on each subplot. During that time, the applied electric voltage was increased from 250 V (10 min) to 300 V, 400 V, 500 V (5 min each), and finally 600 V (10 min). All earthworms that came out of the soil after the application of electric voltage were removed. Many studies have validated the efficiency of this method in reducing earthworm densities for some time (Schmidt, 2001; Eisenhauer et al., 2009; Pelosi et al., 2009). Potential side effects caused by the octet method in comparison to earthworm reduction due to intensification practices cannot be completely excluded. However, based on studies showing negligible side effects of the method (also on soil conditions) (Blair et al., 1995; Čoja et al., 2008; Singh et al., 2016) and the fact that earthworms are not necessarily dying in the soil under intensified management, but could also migrate to more favorable patches in response to frequent disturbances, we are confident to report realistic effects based on variations in earthworm densities.

2.3. Plot management

After a fallow period since August 2009 and manual ploughing by using a spade (November 2009), spring barley (*Hordeum vulgare*, type "Quench") was planted in all experimental plots on March 30th, 2010 (Fig. 1a). To maintain micro-environmental conditions similar to a crop stand, the area in-between the plots was also planted. The plants were fertilized with calcium ammonium nitrate (60 kg N ha^{-1}) on April 29th, 2010 and manually reduced to 290 barley individuals per square meter on May 15th, 2010 to have the same plant density on each plot (to avoid density-dependent effects). In June and July 2010, herbicides (Ariane C by Dow AgroSciences containing Clopyralid, Fluoxypyr, and Florasulam; and Ralon Super by Lotus Agrar GmbH containing Fenoxaprop-P) were applied using a backpack sprayer following the recommendations of 1.5 l ha^{-1} (Ariane) and 1.0 l ha^{-1} (Ralon Super), respectively (both dissolved in 300 l water). The fungicide (Stratego by Bayer AG containing Propiconazol and Trifloxystrobin) was applied at 800 ml ha^{-1} (again dissolved in 300 l of water) as it is often done in comparable agricultural fields in the region. For an overview of the relevant management practices see Table S1.

2.4. Aboveground plant biomass

The harvest of spring barley (*Hordeum vulgare*, type "Quench") was carried out on August 5th, 2010. The plants were sampled within the inner 0.25 m^2 of each subplot, separated into leaves, stems, and ears (the upper grain-bearing part of the stem) before the dry weight was determined. The total aboveground plant biomass is given in grams of dry weight per square meter (Högy et al., 2013).

2.5. Soil microbial biomass and ergosterol

For the measurement of microbial biomass and ergosterol content, three subsamples of the upper 5 cm of the soil were taken from randomized positions per plot (soil corer with 3 cm diameter) on August 24th, 2010. Soil samples were pooled per plot, sieved (at 2 mm), homogenized, and stored at −20 °C until analyses.

To determine microbial biomass C, the chloroform-fumigation-extraction (CFE) method (Vance et al., 1987) was applied: 10 g of fresh soil was fumigated with ethanol-free chloroform in a desiccator at room temperature for 24 h. After this incubation, chloroform was removed and then fumigated and non-fumigated samples were dispersed in 40 ml of 0.5 M K_2SO_4 and extracted on a horizontal shaker at 250 rev min^{-1} for 30 min. Afterwards, the samples were centrifuged for 30 min at 4400 g so that the supernatant could be analyzed for DOC (DIMATOC 100, Dimatec GmbH, Essen, Germany). The supernatant was diluted (1:4 ratio) to avoid a high salt concentration for the subsequent analysis. The DOC contents of the non-fumigated samples served as controls for the CFE analysis, but also as an indication for the K_2SO_4 extractable organic C pool of the soil (Poll et al., 2008). For calculation of microbial biomass a k_{EC} correction factor of 0.45 (Joergensen, 1996) was used.

The extraction of ergosterol was done following Djajakirana et al. (1996): a mixture of 1 g of soil and 50 ml ethanol was first shaken for 30 min on a horizontal shaker at 250 rev min^{-1} before the samples were centrifuged for another 30 min at 4400 g. Then, 20 ml of the sample was put into a centrifugation tube and concentrated to dryness by using a RVC 2–25 (Martin Christ GmbH, Osterode, Germany). In order to remove ergosterol from the walls of the tubes, 3 ml of ethanol was added afterwards and evaporated. The residue was dissolved in 1 ml methanol and put into 2 ml brown glass HPLC vials using 0.45 µm cellulose-acetate filters. Finally, ergosterol was quantified by HPLC analysis (Beckmann Coulter, System Gold 125, Fullerton, USA) with a 150 x 3.0 mm^2 column (MZ-Aqua Perfect C18 3 µm, MZ Analysentechnik GmbH), pure methanol as mobile phase, a flow rate of 0.5 ml min^{-1}, and a detection wavelength of 282 nm. The standard (Sigma-Aldrich, St. Louis, USA) was dissolved in ethanol and diluted to the final concentrations of 0, 0.1, 0.2, 0.5, 1, and 2 µg ergosterol ml^{-1}.

2.6. Protists

Soil samples for protist analyses were taken with a metal corer (5 cm diameter, 10 cm depth) on August 24th 2010. On each subplot, five subsamples were taken from randomized positions; the soil was homogenized and stored at 5 °C until examination. The two major protist morphotypes (naked amoebae and flagellates) were determined according to a modified most probable number method (Darbyshire et al., 1974): 5 g of fresh soil was suspended in 20 ml sterile Neff's modified amoeba saline (NMAS; see Page 1976) on a vertical shaker for 20 min. Then, 96-well microtiter plates (VWR, Darmstadt, Germany) were set up with four replicates for threefold dilution series with nutrient broth (Merck, Darmstadt, Germany) and NMAS at 1:9 v/v. After incubating the microtiter plates at 15 °C in darkness, the presence of amoebae and flagellates in the wells was determined after 3, 6, 11, 19, and 26 days with an inverted microscope at ×100 and ×200 magnification (Nikon, Eclipse TE 2000-E, Tokyo, Japan). Protist densities were calculated according to Hurley and Roscoe (1983) as individuals per gram dry weight soil.

2.7. Nematodes, meso- and macrofauna

The sampling of nematodes was carried out on August 23rd, 2010. By using a small shovel, three random subsamples were taken per plot (~50 g of soil from the upper 10 cm), which were later pooled and homogenized. Additional samples (three subsamples) were taken for measuring soil moisture by weighing the samples before and after drying them at 105 °C for 24 h. A mean soil temperature of 21.1 °C and mean soil water content of 19.25% ensured that fee-living nematodes were active during the sampling. Nematodes were extracted according

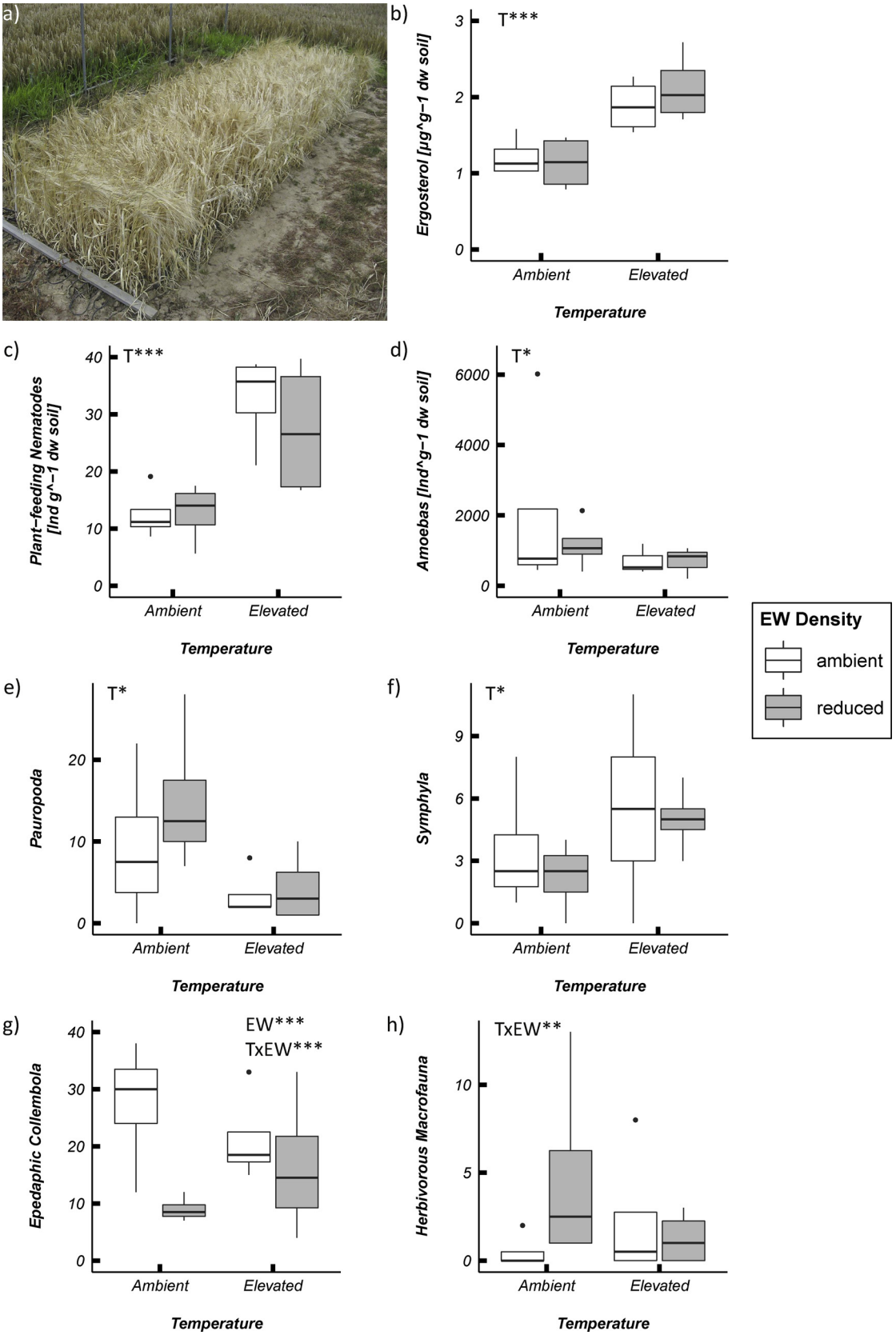

Fig. 1. (a) Experimental plot with barley and heating cables at the University of Hohenheim. Copyright: Christian Poll. Boxplots showing the effects of elevated temperature and reduced earthworm density on (b) ergosterol concentrations, densities of (c) plant-feeding nematodes,(d) Amoeba, (e) Pauropoda (raw counts), (f) Symphyla (raw counts), (g) epedaphic Collembola (raw counts), and (g) herbivorous macrofauna (raw counts). White = ambient earthworm densities; grey = reduced earthworm densities; T = temperature treatment; EW = earthworm treatment. Significance-levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 1
Chi-squared values (χ^2) for the effects of elevated temperature, reduced earthworm density, and their interaction on individual groups of soil organisms, soil diversity, crop yields, and microbial properties. Generalized mixed-effects models with a negative binomial distribution were used for count data (i.e. individual groups of soil organisms, indicated by ^{NB}), whereas linear mixed-effects models were used for soil diversity, crop yields, and microbial properties. Plots nested within blocks served as a random intercept in the models. Significant results are shown in bold.

	Temperature (T)		Earthworm density (E)		T x E	
	chi-square	*p-value*	*chi-square*	*p-value*	*chi-square*	*p-value*
Densities (count data)^{NB}						
Amoebas (Ind g^{-1} dw soil)	**4.81**	**0.03**	0.41	0.52	0.23	0.63
Flagellates (Ind g^{-1} dw soil)	0.81	0.37	0.15	0.70	0.01	0.93
Plant-feeding nematodes (Ind g^{-1} dw soil)	**26.97**	< **0.001**	0.36	0.55	0.34	0.56
Fungal-feeding nematodes (Ind g^{-1} dw soil)	0.23	0.63	1.79	0.18	0.39	0.53
Bacteria-feeding nematodes (Ind g^{-1} dw soil)	2.86	0.09	1.07	0.30	0.03	0.86
Predatory nematodes (Ind g^{-1} dw soil)	0.14	0.71	1.18	0.28	0.06	0.81
Omnivorous nematodes (Ind g^{-1} dw soil)	0.29	0.59	0.00	0.96	1.30	0.25
Total abundance (meso- and macrofauna)	0.09	0.76	0.47	0.49	0.26	0.61
Oribatida	0.25	0.62	0.18	0.67	2.54	0.11
Gamasida	0.91	0.34	2.32	0.13	0.18	0.67
Astigmata/Prostigmata	0.04	0.84	0.82	0.37	0.61	0.43
Pauropoda	**7.56**	**0.01**	0.78	0.38	0.13	0.72
Symphyla	**5.35**	**0.02**	0.78	0.38	0.48	0.49
Diplopoda	0.00	0.98	0.41	0.52	0.51	0.48
Total Collembola	1.78	0.18	0.13	0.72	2.71	0.10
Epedaphic Collembola	0.00	0.97	**24.10**	< **0.001**	**11.28**	< **0.001**
Euedaphic Collembola	2.07	0.15	0.20	0.65	1.44	0.23
Isotomidae	0.04	0.84	2.90	0.09	**6.87**	**0.01**
Sminthuridae	0.00	0.99	**16.81**	< **0.001**	1.87	0.17
Entomobryidae	0.01	0.91	2.18	0.14	0.86	0.35
Onychiuridae	**5.80**	**0.02**	1.44	0.23	1.39	0.24
Predatory macrofauna	2.58	0.11	2.55	0.11	0.13	0.71
Herbivorous macrofauna	0.40	0.53	0.98	0.32	**9.10**	< **0.01**
Diversity measures						
Taxon richness (all)	1.59	0.21	0.29	0.59	0.81	0.37
Taxon richness (nematodes)	1.30	0.25	0.02	0.90	0.15	0.69
Taxon richness (meso- and macrofauna)	0.50	0.48	2.07	0.15	**7.14**	**0.01**
Shannon diversity (meso- and macrofauna)	0.48	0.49	0.99	0.32	0.03	0.86
Simpson diversity (meso- and macrofauna)	0.00	0.99	0.13	0.72	0.01	0.92
Pielou's evenness (meso- and macrofauna)	0.12	0.72	0.30	0.59	0.38	0.54
Crop yields and microbial properties						
Spring barley (g m^{-2})	0.44	0.51	0.18	0.67	0.02	0.90
Microbial biomass (µg g^{-1} dw soil)	0.03	0.86	0.06	0.80	0.56	0.45
Ergosterol (µg g^{-1} dw soil)	**20.83**	< **0.001**	0.19	0.67	0.75	0.39

to a modified Baermann method (Ruess, 1995), fixed in 4% formaldehyde solution and stored at 8 °C until microscopic examination. The nematodes were identified up to genus level and assigned to five trophic groups, according to Yeates et al. (1993) based on their mouthpart morphology: plant feeders, fungal feeders, bacterial feeders, predators, and omnivores. Densities were expressed as individuals per gram dry weight soil.

On August 24th, 2010, the soil sampling for the meso- and macrofauna was performed by using a steel corer (diameter 22 cm, depth 10 cm) and taking one soil core per plot. The soil animals were extracted by the heat extraction method according to Kempson et al. (1963), collected in diluted glycerol, and transferred into ethanol (70%), where they were stored until examination. Identification and counting was done by using a binocular microscope based on relevant identification literature (Hannemann et al., 2000; Schaefer, 2000; Hopkin, 2007). Apart from the densities of the single taxa, diversity indices were calculated and some taxa were grouped to serve as additional variables: For the meso- and macrofauna, we calculated Pielou's measure of species evenness, Shannon diversity, Simpson diversity, and taxon richness using the package "*vegan*" (Oksanen et al., 2013). The diversity measures were calculated with the highest taxonomic resolution available for the data, i.e., for nematodes, the diversity measures were calculated on genus level, for meso- and macrofauna they were calculated on family level or suborder level. Furthermore, we grouped the following taxa as "Predatory macrofauna": Araneae (6.90% by abundance), Lithobiidae (20.69%), Geophilidae (24.14%), Coleoptera larvae (24.14%), Carabidae (10.34%), Staphylinidae (10.34%), and Staphilinidae larvae (3.45%). Likewise, Oniscidea (5.71% by abundance), Elateridae larvae (5.71%), Curculionidae (2.86%), Thripidae (65.71%), and Sternorrhyncha (20.00%) were grouped as "Herbivorous macrofauna". Collembola were divided into surface-dwelling epedaphic and soil-dwelling euedaphic specimen.

The sampling methods used in the present study are standard approaches used in soil ecology that were developed to evaluate and compare densities of micro-, meso-, and macrofauna (Kempson et al., 1963; Darbyshire et al., 1974; Vance et al., 1987; Ruess, 1995; Djajakirana et al., 1996; Eisenhauer et al., 2013) and which should be appropriate for comparisons of soil organisms across different body sizes. For an overview of all soil samplings see Table S1.

2.8. Data analysis

The responses of microbial properties, crop yields, and soil diversity measures to temperature, earthworm density, and their interaction were analyzed using linear mixed-effects models with the *nlme* package (Pinheiro et al., 2016). Plots were nested within blocks and incorporated as random intercepts in all models. For all the count data (i.e. the density of animal groups), we used generalized linear mixed-effects models within the *lme4* package (Bates et al., 2015) with negative binomial error terms (due to overdispersion (residual deviance > > degree of freedom) when modelled with Poisson error terms). Further, the count data was generally treated as raw counts without

transformations per unit sampling area. In the case of transformed count data (i.e. protists and nematodes are expressed as individuals per g dry weight soil), the densities were rounded to integer numbers prior to analysis. Model assumptions were diagnosed using Shapiro-Wilk test for the normality of model residuals and Levene's test of homogeneity of the variance. All statistical analyses were carried out in the R statistical software version 3.5.0 (R Core Team, 2018).

3. Results

3.1. Treatment effects

The treatment proved to be efficient in increasing the soil temperature at 4 cm depth by 1.6 °C from beginning of January to end of August 2010 (+2.1 °C from June – August 2010 due to lower heat loss over summer) (Fig. S2a). At the specific fauna sampling dates soil temperature was 11% higher at elevated temperature plots (Fig. S2b). Soil water content was decreased by 8% (ambient versus elevated temperature plots) from beginning of January to end of August 2010 (−11% from June to August 2010) (Fig. S2c). Measurements of gravimetric water content during the fauna sampling revealed that both experimental treatments interactively affected soil moisture. Lowest levels were reached under elevated temperature and reduced earthworm density (−17% compared to ambient conditions; Fig. S2d).

3.2. Microbial, plant, and soil invertebrate responses

Elevated temperature increased the amount of ergosterol at both levels of earthworm density (+70% compared to control; Fig. 1b, Table 1). However, we did not find any significant change in total microbial biomass C or in barley yields (Fig. S3a). Plant-feeding nematodes were the only nematode feeding group significantly changing in response to any of the treatments. They were significantly higher in densities at elevated temperature than at ambient temperature (+138%; Fig. 1c). Furthermore, Amoeba (−56%, Fig. 1d) and Pauropoda (−68%, Fig. 1e) declined at elevated temperature, whereas Symphyla (+83%, Fig. 1f) and Onychiuridae (+70%, Fig. S3b) showed higher densities at elevated temperature.

We also detected significant interactions between elevated temperature and reduced earthworm densities: surface-dwelling (epedaphic) Collembola had the highest density at ambient conditions, which strongly declined under reduced earthworm densities under ambient temperature (−67%, Fig. 1g). At elevated temperature, ambient and reduced earthworm densities led to intermediate levels of epedaphic Collembola densities; again with a negative, however less pronounced, effect of reduced earthworms. A closer look at Collembola families revealed that Isotomidae (also with significant interactive effects of temperature and earthworm density; Fig. S3c) showed the same patterns as the group of epedaphic Collembola. The strong decline of Sminthuridae densities (−53%, Fig. S3d) was largely accountable for the strong decline in epedaphic Collembola under reduced earthworm densities. In contrast, the density of herbivorous macrofauna was increased in the reduced earthworm treatment (+950%, Fig. 1h). Their increase caused by the reduced earthworm treatment was weaker under elevated temperature (+250% compared to +950%).

3.3. Responses of belowground diversity

The main effects of elevated temperature and reduced earthworm density on the diversity measures of soil meso- and macro-fauna were non-significant (Table 1). However, we found a significant interactive effect of elevated temperature and reduced earthworm density on the taxon richness of the meso- and macrofauna (Fig. 2a): elevated temperature decreased taxon richness when earthworm densities were reduced (−12%), but increased taxon richness at ambient earthworm densities (+8%). Other metrics of biodiversity did not show any significant response to elevated temperature and earthworm density (Table 1). For instance, we did not find any significant changes in total taxa richness or in nematode taxon richness in response to elevated temperature and earthworm density treatments (Fig. 2b).

All means and standard errors are provided in Table S2. For estimates and intercepts of each response variable see Table S3.

4. Discussion

In order to secure ecosystem functioning and food provisioning in the future, humankind depends on agricultural systems that can resist the detrimental effects of climate change (Orrell and Bennett, 2013; Pachauri et al., 2014; Masson-Delmotte et al., 2018). Soil biota play a crucial role in sustainably maintaining productive agriculture (Wall et al., 2015). Our experiment showed that different groups of soil organisms vary in their vulnerability to climate warming and lower earthworm densities (as a proxy for land-use intensification). Specifically, we found that the diversity of soil meso- and macrofauna was lowest at elevated temperature and reduced earthworm densities. Such critical shifts in the structure of soil food webs point to potential alterations in future ecosystem functioning.

4.1. Microbial and protist responses

Greater concentrations of ergosterol at higher temperature indicated that fungal biomass was enhanced under warmed soil conditions. Similar effects of temperature on fungal communities have been shown in previous studies (Ruess et al., 1999; Clemmensen et al., 2006; Thakur et al., 2017a), suggesting that rapid increases in fungal production can exceed consumption by soil fauna in warmer environments. This supports the notion that warming can potentially enhance nutrient cycling and decomposition rates when other edaphic resources are not limiting, such as soil moisture (Hobbie, 1996; Davidson and Janssens, 2006).

Warming decreased the abundance of Amoeba, whereas flagellates were not affected by any of the treatments. This is alarming as protists are generally well adapted to changing soil moisture levels by rapid encystation, and the MPN method (most probable number) estimates the protist numbers hatching from accumulated cysts rather than active protists (Ekelund and Rønn, 1994). While other studies have clearly demonstrated increased abundances of amoebae and flagellates in earthworm burrow walls and cast material (Geisen et al., 2014; Andriuzzi et al., 2016), these microhabitats will not be preserved in bulk soil samples of agricultural soils, explaining the lack of facilitating effects in our study system.

4.2. Microarthropod responses

Previous studies have shown that the sensitivity to climate warming increases with trophic level from plants to predators (Voigt et al., 2007; Hines et al., 2015). However, we could not detect any treatment effects on the highest trophic levels (predatory nematodes and macrofauna), which was surprising given the typically high vulnerability of predators to warming, which can for example be related to greater metabolic demands compared to lower trophic levels (Petchey et al., 1999; Fussmann et al., 2014). At lower trophic levels (herbivores and detritivores), in contrast, we saw variation in the susceptibility to climate among taxa. For example, while warming decreased the abundance of Pauropoda, our results revealed that the effects of soil warming were positive on certain groups of soil organisms, namely on Symphyla and plant-feeding nematodes. These results may be, in part, due to the sensitivity of the basal trophic level. There is mounting evidence in the literature that warmed soils are associated with higher plant biomass production (Kardol et al., 2010a; Lin et al., 2010), which may subsequently lead to improved food availability for herbivorous species, thereby sustaining their greater population size. However, we could not

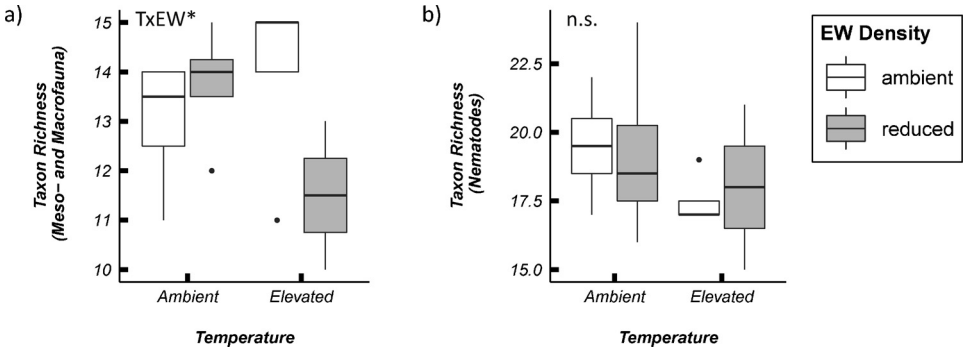

Fig. 2. Boxplots showing the effects of elevated temperature and reduced earthworm density on (a) the taxon richness of meso- and macrofauna, and on (b) the taxon richness of nematodes. White = ambient earthworm densities; grey = reduced earthworm densities; T = temperature treatment; EW = earthworm treatment. Significance-levels: n.s. = not significant, $p > 0.05$*.

find a significant increase in aboveground barley biomass at elevated temperature in our experiment (Fig. S3a, Table 1), suggesting that there were other mechanisms involved causing the positive effect on plant-feeding nematodes, such as elevated root biomass or lower plant defense. We could also speculate that warming-induced increases in plant-feeding nematodes may have diminished the expected increase in barley production under warmed condition and increased the crop plants' vulnerability to other pathogens (Trudgill, 1991; Moens and Perry, 2009). Studies in natural ecosystems reported a relative decline in plant-feeding nematodes, compared to microbial-feeding nematodes under experimental warming in the temperate-boreal forest ecotone (Thakur et al., 2014), or in a semiarid grassland (Mueller et al., 2016). Interestingly, our opposing results were derived from an agricultural study system and could provide evidence that warming can potentially enhance belowground herbivory in intensively managed systems. This is of particular importance since plant-feeding nematodes are known as important pests in agricultural fields that can cause severe reductions in crop production (Evans et al., 1993). In agricultural systems, where host plant quality is greatly enhanced due to fertilization, damage by plant-feeding nematodes may increase under climate change as shown for rice under elevated CO_2 (Hu et al., 2017).

Our prediction that the presence of earthworms leads to higher abundances of other soil organisms, could only be confirmed for surface-dwelling epedaphic Collembola species (and for Sminthuridae within this group): reduced earthworm density had a strong negative impact on their abundance at both temperature levels, even though more pronounced at ambient temperature. The decline of epedaphic Collembola probably relates to their dependence on the structures and microhabitats typically formed by earthworms, which could be even more crucial for the sustenance of surface-dwelling soil organisms in disturbed agricultural soils (Brown, 1995). We therefore suspect that epedaphic soil organisms might be amongst the most susceptible taxa under a future scenario of intensified agriculture. Epedaphic Collembola occur in very high numbers throughout the upper soil layers, represent important prey organisms for higher trophic level predators, and contribute to nutrient cycling (Filser, 2002; Coleman et al., 2004). Thus, their decline can induce bottom-up shifts by potentially promoting fungi in the soil, given that Collembola are important fungal grazers belowground (Coleman et al., 2004; Von Berg et al., 2010).

Herbivorous macrofauna was the group that benefitted from the absence of earthworms, especially at ambient temperature levels. This may be due to the activity of earthworms constantly moving plant material into deeper soil layers (van Vliet and Hendrix, 2003), thus making it more difficult to access for larger herbivorous species (e.g., woodlouse or thrips), which primarily live close to the soil surface (Coleman et al., 2004; Eisenhauer et al., 2007). As plant biomass is likely to be reduced under warmed and thus dryer conditions (Fig. S2), the effect was less pronounced compared to ambient temperature levels. Overall, this suggests that the soil structures created by earthworms are indeed of particular importance for smaller soil animals, whereas larger species may be at advantage when earthworms are reduced. The fact that only two taxa (groups) responded to the earthworm reduction treatment may indicate that the reduction was less strong than intended by the experimental setup. It could be that earthworms partly re-colonized the plots within the five months between the last earthworm extraction (March 2010) and the fauna sampling (August 2010), thereby weakening the effects on less susceptible taxa. Nevertheless, the efficiency of the earthworm treatment is reflected in the lowest soil water content (Fig. S2d). Moreover, our results highlight the complex interplay between ecosystem engineers and climate warming in shaping key soil abiotic characteristics, such as soil water content, which subsequently determine biotic responses in the soil.

4.3. Diversity responses

Temperature and earthworm density exerted a significant interactive effect on the taxon richness of meso- and macrofauna. While elevated temperature increased taxon richness at ambient earthworm densities, taxon richness substantially declined in combination with reduced earthworm density. This may be due to detrimental soil conditions for many species: while warming potentially decreases soil moisture through higher evapotranspiration (Dermody et al., 2007), lower earthworm densities may further reduce taxon richness by reducing important microhabitats (Eisenhauer, 2010). We could speculate that these negative effects of the treatment combination (warming x reduced earthworms) leading to the lowest taxon richness were partly caused by mobile organisms escaping the unfavorable soil conditions by moving to deeper soil layers (Briones et al., 2007), thus leading to particularly low numbers of detectable taxa in our study.

The highest diversity of meso- and macrofauna was found at elevated temperature and ambient earthworm densities (supporting our hypothesis iii). Thus, the presence of earthworms may have contributed to reverse the negative effects of warming on taxon richness into a slight net positive effect. This corresponds to a recent study revealing that complex soil environments can buffer the detrimental effects of warming on species diversity (Thakur et al., 2017b). In our study, we found the lowest soil water content at elevated temperature and reduced earthworm densities, providing support that greater organic matter in earthworm casts may have sustained greater soil water content, in turn buffering the drying effects of warming on soil fauna (Fig. S2d). Surprisingly, reduced earthworm density also led to higher taxon richness compared to ambient earthworm levels, but only at ambient temperature. This finding is in line with the observation that the presence of earthworms can also be detrimental to some microarthropod species, due to their direct competition for limiting resources and the creation of unfavorable soil conditions (e.g., drought, disturbances) (Brown, 1995; Eisenhauer, 2010). Under ambient climatic conditions, the structures created by earthworms, such as burrows and channels, may prevent direct encounters, since species can successfully hide and escape predation (Salmon et al., 2005). Under elevated temperature, earthworm structures become particularly important for species to find

shelter and avoid adverse soil conditions like water shortage. Despite some notable limitations of our study, such as limited sample size and taxonomic resolution, and the artificial reduction of earthworms to simulate intensified management, the loess-derived stagnic Luvisol found at the experimental site may have buffered the effects of our warming treatment to a certain extent by preventing water run-off to deeper soil layers, thus protecting the sampled soil layers from desiccation. We encourage future studies to build on the present findings and especially examine how earthworms differing in life history traits (e.g., in feeding and burrowing behavior) may vary in their capacity to buffer the warming effects on soil organisms.

5. Conclusions

Overall, our findings suggest that agricultural systems may experience shifts in soil community composition and a decline in species diversity in a warmer world. Notably, significant interactive effects of warming and intensified land-use (as simulated by reduced earthworm density) may alter the functioning and service provisioning of soils. This is alarming given that greater soil biodiversity is key to ensure crop productivity and crop quality, and to improve the resilience of ecosystems against changing environmental conditions. Our results show that the presence of earthworms partially mediate the responses of certain groups of soil organisms to warming. Importantly, we show that the diversity of micro-arthropod communities in the soil can be maintained under warmed conditions as long as high densities of earthworms are present. Accordingly, we conclude that agricultural management supporting high earthworm densities can partly mitigate climate effects on some of the components of soil biodiversity, namely soil meso- and macrofauna, which are crucial for the provisioning of sustainable agricultural production.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2019.03.004.

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